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Segregation distortion via male gametes in hybrids between Indica and Japonica or wide-compatibility varieties of rice (*Oryza sativa* L)

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Summary. One or two marker genes on each of chromosomes 3, 4, 6, 7, 8, 11 and 12 of the 12 rice chromosomes were tested for segregation distortion in indica-japonica hybrids. Marker genes on chromosomes 3, 7, 8, 11 and 12 showed clear segregation distortion. This distortion was not related to the proportion of normal pollen. The germinability of the pollen was less than 10% in the hybrids, although 45–55% of the pollen grains appeared to be morphologically normal. The frequent occurrence of segregation distortion and the low germinability of the pollen grains suggested that a large portion of the pollen produced by the Indica-Japonica hybrids was not functional. The fact that the segregation distortion of the same marker may be positive or negative depending on the cross combination suggested the existence of multiple alleles, including distortion-neutral alleles. The latter mitigate pollen sterility in certain hybrid combinations.

Key words: Rice – Segregation distortion – Wide cross – Pollen sterility – Wide compatibility variety

Introduction

Segregation distortion has been frequently reported in wide crosses of rice (Nakagahra 1972; Nakagahra et al. 1972; Nakagahra 1985; Maekawa et al. 1981; Maekawa and Kita 1985). A number of genetic markers have been found to show segregation distortion in wide crosses. More recently, many instances of segregation distortion have been reported through studies of isozymes (Ishikawa et al. 1987a, b; Ranjhan et al. 1988; Wu et al. 1988; Guiderdoni et al. 1989) and RFLP alleles (McCouch et al. 1988; Saito et al. 1991). The genetic basis of the segregation distortion may be the abortion of male or female gametes or selective fertilization of particular gametic genotypes. To date most studies have not investigated the mechanisms responsible for segregation distortion.

It is desirable to know the extent and genetic basis of segregation distortion in wide crosses. Ikehashi and Araki (1986, 1988) reported that multiple alleles at a locus on chromosome 6 interact with each other to condition partial female gamete abortion, which is expressed as semi-sterility of the panicle. The $S\text{-}5^i$ and $S\text{-}5^j$ alleles are present in Indica and Japonica cultivars, respectively, and $S\text{-}5^n$ is present in cultivars with wide compatibility. Gametes carrying the $S\text{-}5^j$ allele are aborted in plants of the genotype $S\text{-}5^i/S\text{-}5^j$, while the neutral allele ($S\text{-}5^n$) from wide compatibility cultivars does not cause female gamete abortion in the heterozygote plants $S\text{-}5^i/S\text{-}5^n$ and $S\text{-}5^j/S\text{-}5^n$. The $S\text{-}5^n$ allele has been successfully used to overcome hybrid sterility in Indica-Japonica crosses.

In contrast to the ease of gaining an understanding of female gamete abortion, male gamete abortion is more difficult to study. The difficulty resides in assessing pollen viability. Pollen fertility is generally studied on the basis of stainability of the pollen grains. However, when pollen fertility was assessed in this manner in rice crosses, it was difficult to relate it to segregation distortion. In the light of what is known about the genetics of female gamete abortion it is considered likely that male gamete abortion is caused by a similar genetic mechanism involving allelic interaction at one or more loci.

In the study presented here two precautions were taken to examine the extent of segregation distortion attributable to the male gametes. First, only those hybrid populations were chosen in which female gamete abortion was attributable only to allelic interaction at the *S-5*

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locus. Thus, any segregation distortion of marker genes except for those near the *S-5* locus could be attributed to the behavior of male gametes. Secondly, we studied segregation distortion in hybrids between indica and 'Wide-Compatibility varieties' that show no female abortion and are known to produce morphologically normal pollen.

The initial results indicated that segregation distortion via the male gamete occurred for at least three or four marker genes on different chromosomes. The extent of segregation distortion was greater than could be predicted on the basis of morphological evaluation of pollen fertility in hybrids. It is also noteworthy that the segregation of a marker gene was often distorted in one cross combination but not in another, thus supporting the hypothesis of multiple alleles, including neutral ones, as the possible cause of segregation distortion. The use of neutral alleles should offer a partial solution for the problem of pollen sterility in Indica-Japonica hybrids.

The term "gametophyte gene" will be used in this paper to refer to male gamete abortion only, following the terminology used in the previous reports.

Materials and methods

Varieties evaluated

'IR29', 'IR36' and 'IR50' were used as Indica varieties; 'Akihikari' (AK) 'Taichung 65' (T65), 'Akamai 1', 'Kamairazu' (KA) and 'FL123' were chosen as Japonica varieties. These varieties were chosen because they have several morphological marker genes and because we have information on the level of sterility observed in their F_1 hybrids. Spikelet sterility in the Indica-Japonica hybrids involving these varieties is due to heterozygosity at the *S-5* locus. The segregation distortion that results from this sterility is observed in marker genes linked to *S-5* and is attributable to female gamete abortion. *S-5* is located between *C* (Apiculus color) and *wx* (waxy endosperm) on chromosome 6 (Ikehashi and Araki 1986).

Three Javanica varieties, namely, 'Calotoc', 'Ketan Nangka' (KN) and 'CPSLO-17', were also included in this study. They are known to possess a neutral allele at the *S-5* locus, and show no spikelet sterility when crossed to either Indica or Japonica varieties (Ikehashi and Araki 1986). These varieties are referred to as wide-compatibility varieties (WCV). In addition, we included a Japonica experimental line, 'Nekken 1', into which the neutral allele from the Javanica KN had been introgressed. Parental materials used and their marker traits are listed in Table 1.

Segregation distortion

Segregation distortion was examined at marker loci in four types of populations (Table 2). In each population segregation at several isozyme and marker gene loci was recorded, but not all markers could be scored in all populations. Isozymes were analyzed according to the methods of Ishikawa et al. (1989).

In the first set of crosses, segregation distortion was examined in F_2 populations derived from semi-sterile F_1 hybrids. In these populations, spikelet sterility was attributable solely to allelic interaction at the *S-5* locus. In the second set, segregation distortion was tested in backcross populations in which the F_1 of Indica-Japonica hybrids was used as the pollen parents in crosses to Indica or Japonica parents. In the third set, F_2 populations derived from F_1 hybrids with normal spikelet fertility were studied. The normal fertility was due the presence of the neutral *S-5*^{n} allele contributed by the Javanica varieties. In the fourth set of crosses, we tested the relationship between pollen fertility and segregation distortion. Top crosses were studied for this purpose. The first single cross in the three-way crosses produced only morphologically normal pollen so that in the population derived from the three-way cross, a 1:1 segregation of plants with normal pollen and those with a reduced ratio of normal pollen was expected.

The F_2 segregation data were tested by a χ^2 test for fitness to a segregation ratio of 3:1 (for morphological markers) or 1:2:1 (for isozyme markers). The backcross and three-way cross populations were tested for fitness to a 1:1 ratio. The distortion ratios were calculated for those markers that showed significant segregation distortion (Table 3).

Table 1. Parental materials studied and their marker gene constitution[a]

Varietal type	Variety	*Pgi-1*	*bc-1*	*ph*	*lg*	*Amp-3*	*Pgi-2*	*Cat-1*	*Rc*	*Est-9*	*Amp-2*	*Pgd-1*	*la*	*Acp-1*
Japonica	Akihikari	2	+	+	+	1	1	2	+	1	1	1	+	+9
	Tatumimoti	2	+	+	+	1	1	2	+	1	1		+	+9
	Akamai 1	2	+	+	+	1	1	2	Rc	1	1		+	+9
	Kamairazu	2	bc	+	+	1	1	2	+	1	1		+	+9
	Taichung 65	2	+	+	+	1	1	2	+	1	1	1	+	+9
	Nekken 1		+	+	+	1	1	2	+	1	1		+	+9
	FL123		+	+	lg	1							la	
Indica	IR29	1	+	Ph	+	1	2	1	+	2	2	2	+	−4
	IR36	1	+	Ph	+	1	2	1	+	2	2	2	+	−4
	IR50	1	+	Ph	+	1	2	1	+	2	2	2	+	−4
WCV (*S-5*^{n})	Calotoc	2	+	+	+	2	1	2	+	1	1		+	+9
	CPSLO-17	2	+	+	+	2	1	2	+	1	2	1	+	+9
	Ketan Nangka	2	+	+	+	2	1	2	+	1	1		+	+9

[a] The symbols of isozyme markers according to Ishikawa et al. (1989). On other loci, bc, lg and la are recessive. Ph and Rc are dominant

Table 2. Marker genes tested for segregation distortion in F_2 and backcross combinations

Crosses[a]	Population sizes	Chromosome number and marker genes												
		3		4		6			7		8	11		12
		Pgi-1	*bc-1*	*ph*	*lg*	*Amp-3*	*Pgi-2*	*Cat-1*	*Rc*	*Est-9*	*Amp-2*	*Pgd-1*	*la*	*Acp-1*
		F_2 of Indica-Japonica crosses												
T65/IR50	130–134	*								**				**
F1123/IR50	124				ns								ns	
Akamai1/IR50	219–229			ns					ns	**				
Nekken1/IR36	116–173			**						**				**
		Backcross with pollen of Indica-Japonica crosses												
AK//AK/IR50	60–96	ns					ns	ns		**		**		*
IR50//AK/IR50	41–43	ns					ns	ns		ns		**		**
IR36//AK/IR50	48–72	ns					ns	ns		**		ns		**
IR36//T65/IR29	34–39							ns		*	ns	*		ns
IT50//TA/IR50	156–162									**	ns	ns		
		F_2 of Indica-Wide Cross varieties												
KN/IR36	91–152	ns				ns	(**)[b]			**	**			ns
IR36/Calotoc	140–149					(**)[b]	ns			ns	**			**
IR36/CPSLO-17	128–226						(*)[b]			**				ns
		Crosses for testing segregation for bc-1												
IR36//KA/Calotoc	51		ns											
KA//KA/IR50	51–52		**	ns										
IR50//KA/IR50	16		**											

*, ** Significant deviation from 1:2:1 or 1:1 at 5% and 1% levels, respectively. ns, Not significant

[a] T65, 'Taichung 65'; AK, 'Akihikari'; TA, 'Tatumimoti'; KN, 'Ketan Nangka'; KA, 'Kamairazu'

[b] ( ): Significant by χ^2, but the segregation between Indica-type gametes and Japonica-type gametes is not distorted

Measurement of pollen fertility and viability

Pollen fertility of Indica-Japonica hybrids was evalauted morphologically by staining the pollen with acetocarmine and observing it under the microscope at a magnification of 200× (Fig. 1A, B). It has been recorded earlier that indica-japonica hybrids show a pollen sterility of about 45–55% on the basis of stainability. The hybrids between WCV (KN, 'Calotoc', 'CPSLO-17') on one hand and either Indicas or Japonicas on the other show normal pollen fertility (Ikehashi and Araki 1984). Pollen germinability (Fig. 1C, D) was tested on an artificial medium.

Results

Distribution of segregation distortion

Segregation ratios for one or two marker genes on each of chromosomes 3, 4, 6, 7, 8, 11 and 12, were examined (Table 3).

Segregation distortion was observed for *bc-1* on chromosome 3 in the crosses 'Kamairazu'//'Kamairazu'/'IR50' and 'IR50'//'Kamairazu'/'IR50'. A predominance of the Indica allele (84–94%) was observed in these crosses. This distortion has been attributed to the segregation of gametophyte gene *ga-2* (Nakagahra 1972; Nakagahra et al. 1972). Segregation distortion was not observed in the hybrid 'IR36'//'Kamairazu'/'Calotoc' (WCV), in which the F_1, 'Kamairazu'/'Calotoc', produced morphologically normal pollen. We suspect that 'Calotoc' may have two neutral alleles; one governing male gamete abortion at the *ga-2* locus, and the other governing female gamete abortion at the *S-5* locus.

A gametophyte gene, *ga-6*, located near *lg* on chromosome 4 causes gamete abortion in Japonica-Japonica hybrids (Maekawa et al. 1981). In the experiment reported here, no segregation distortion was observed at the *lg* locus in an F_2 population derived from an Indica-Japonica hybrid, 'FL123'/'IR50' (Table 2). Only one case of distorted segregation for a marker of chromosome 4 (*Ph*) was observed in a 'Nekken 1'/'IR36' F_2 population (Table 3).

The segregation distortion of markers on chromosome 6 was found to be caused by allelic interaction at the *S-5* locus. When pollen from F_1 hybrids were used for backcrossing, no segregation distortion was found for three markers on chromosome 6, two of which are near the *C-wx* segment (Table 2). This confirmed the earlier finding that the segregation distortion of markers on chromosome 6 is caused through partial female gamete abortion in Indica-Japonica hybrids.

Segregation of *Est-9* on chromosome 7 was significantly distorted in almost all of the crosses studied, with a low transmission rate of the allele from Indicas (Table 3). The transmission ratio of the Indica allele at the *Est-9* locus was 0.17–0.37, lower than the expected 0.5. Al-

Table 3. Estimation of segregation distortion for each marker gene in different cross combinations

Crosses[a]	Segregation			TRRA[b] of Indica type (%)	*P*
	II	H	JJ		
	bc-1 (chromosome 3)				
IR36//KA/Calotoc	25	26		49±14	0.8–0.9
KA//KA/IR50		43	8	84±10**	<0.01
IR50//KA/IR50	15	1		94±12**	<0.01
	Pgi-1 (chromosome 3)				
T65/IR50	48	67	19	72±11**	<0.01
KN/IR36	33	61	25	57±13	0.5–0.7
AK//AK/IR50		41	56	42±10	0.1–0.2
IR50//AK/IR50	15	28		35±14*	0.02–0.05
IR36//AK/IR50	38	34		53±12	0.5–0.7
	ph (chromosome 4)				
Akamai1/IR50		162	67	41± 9	0.1–0.2
Nekken1/IR36		72	54	14± 9**	<0.01
KA//KA/IR50		20	32	38±13	0.05–0.1
	Cat-1 (chromosome 6)				
AK//AK/IR50		35	44	44±11	0.3–0.5
IR50//AK/IR50	18	25		42±15	0.2–0.3
IR36//AK/IR50	34	38		47±12	0.5–0.7
IR36//T65/IR29	22	12		65±16	0.05–0.1
	Pgi-2 (chromosome 6)				
IR36/Calotoc	41	76	30	58±11	0.3–0.5
KN/IR36	36	35	34	51±12**	<0.01
IR36/CPSLO-17	36	94	25	59±12*	0.01–0.02
AK//AK/IR50		45	36	56±11	0.3–0.5
IR50//AK/IR50	18	25		42±15	0.2–0.3
IR36//AK/IR50	32	40		44±11	0.3–0.5
	Amp-3 (chromosome 6)				
IR36/Calotoc	29	93	27	52±13**	<0.01
KN/IR36	34	86	31	52±12	0.2–0.3
	Est-9 (chromosome 7)				
T65/IR50	16	75	40	29±12**	<0.01
Akamai1/IR50	34	102	83	29± 8**	<0.01
Nekken1/IR36	15	27	74	17± 8**	<0.01
KN/IR36	26	72	54	33±10**	<0.01
IR36/Calotoc	24	79	41	37±12	0.05–0.1
IR36/CPSLO-17	31	113	82	27± 8**	<0.01
AK/AK/IR50		25	71	26± 9**	<0.01
IR50//AK/IR50	16	27		37±14	0.05–0.1
IR36//AK/IR50	26	46		36±11*	0.01–0.02
IR36//T65/IR29	7	32		18±12**	<0.01
IR50//TA/IR50	41	119		26± 7**	<0.01
	Amp-2 (chromosome 8)				
IR36/Calotoc	54	56	38	59±10**	<0.01
KN/IR36	37	44	13	74±12**	<0.01
IR36//T65/IR29	14	25		36±15	0.05–0.1
IR50//TA/IR50	69	87		44± 8	0.1–0.2
	Pgd-1 (chromosome 11)				
AK//AK/IR50		41	20	67±12**	<0.01
IR50//AK/IR50	30	13		70±14**	<0.01
IR36//AK/IR50	21	27		44±14	0.3–0.5
IR36//T65/IR29	10	29		26±14**	<0.01
IR50//TA/IR50	87	75		54± 8	0.3–0.5

Table 3. (continued)

Crosses[a]	Segregation			TRRA[b] of Indica type	*P*
	II	H	JJ		
	Acp-1 (chromosome 12)				
T65/IR50	45	68	17	73±11**	<0.01
Nekken1/IR36	61	65	47	56± 9**	<0.01
IR36/Calotoc	51	57	32	61±10**	<0.01
KN/IR36	23	46	22	51±15	0.98–0.99
IR36/CPSLO-17	30	69	29	51±13	0.5–0.7
AK//AK/IR50		22	38	37±12*	0.02–0.05
IR50//AK/IR50	10	31		24±13**	<0.01
IR36//AK/IR50	21	46		31±11**	<0.01
IR36//T65/IR29	24	15		62±15	0.1–0.2

*,** Significant deviation from 1:2:1 or 1:1 at 5% and 1% levels, respectively

[a] T65, 'Taichung 65'; AK, 'Akihikari'; TA, 'Tatumimoti'; KN, 'Ketan Nangka'; KA, 'Kamairazu'

[b] TRRA, Transmission ratio, for which confidence intervals were calculated at 95% levels

though no gametophyte gene has been reported on chromosome 7, the existence of such a gene near the locus of *Est-9* seems likely.

Segregation distortion for *Amp-2* on chromosome 8 was also significant in the F_2 population derived from the Indica/WCV ('IR 36'/'Calotoc') hybrid. In this cross, no female gamete abortion was observed, and the pollen from the F_1 is morphologically normal (Ikehashi and Araki 1984). Thus, the relationship between pollen fertility and segregation distortion remains unclear. No distortion of this marker was observed in a typical Indica-Japonica hybrid, i.e., T65/'IR29', suggesting that Japonica varieties may possess a neutral allele for the gametophyte gene that apparently exists near this locus.

The segregation distortion found for *Pgd-1* on chromosome 11 was observed in backross progeny when pollen of the Indica-Japonica F_1 was used for making the backcross. This result suggests that a gametophyte gene may also be present near this isozyme locus. However, a larger population is needed to confirm these results, and other crosses should be examined to determine the nature of this gametophyte gene.

The segregation distortion for *Acp-1* on chromosome 12 was clear in most of the crosses examined. It is also noteworthy that the ratio of heterozygotes to homozygotes was lower than the expected 50% in the F_2s of the crosses 'Nekken1'/'IR36' and 'IR 36'/'Calotoc' (Table 3). No distortion was observed in the crosses KN/'IR36' and 'CPSLO-17'/'IR36', which produced morphologically normal pollen, thus indicating that the WCV varieties KN and 'CPSLO-17' may be donors of a neutral allele of the gametophyte gene.

A triple cross, 'Calotoc'/'IR36'//'Akihikari' showed both the segregation of plants with normal pollen and

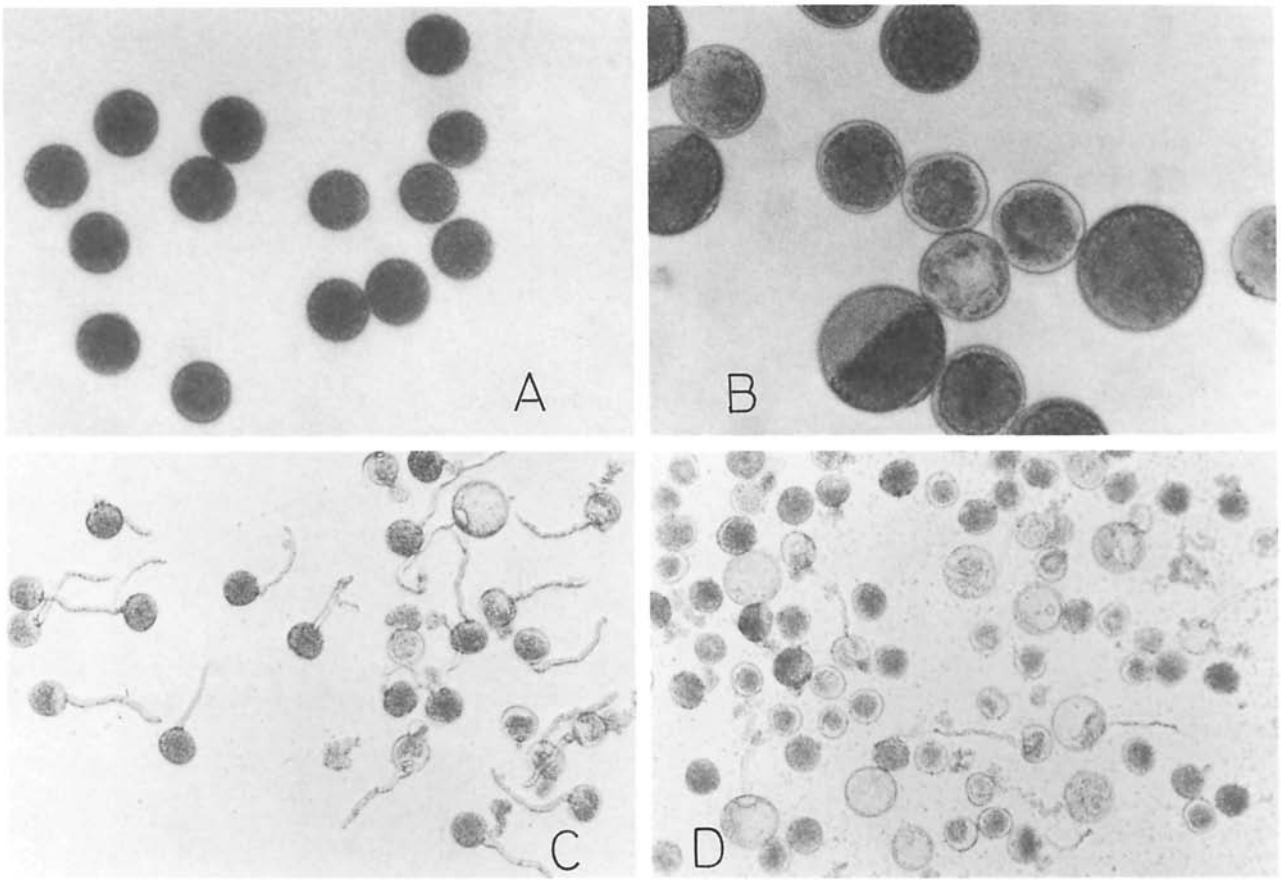

Fig. 1. Evaluation of pollen fertility. **A** and **B** were observed by staining with acetocarmine; *C* and *D* were observed in an artificial medium (Ishikawa unpublished). **A** and **C** show the pollen of the parental varieties; *B* and *D* show the pollen of typical Japonica and Indica hybrids

Table 4. Relationship between pollen fertility and marker genes in 'IR36'/'Calotoc'//'Akihikari'

Marker genes	Distribution of pollen fertility (%)[a]						Total number of plants	Mean fertility
	50	60	70	80	90	100		
C^+/C^+			7	4	8	15	34	83.8
C/C^+	1	2	5	4	5	12	29	81.0
Amp-3^{11}			6	5	6	16	33	84.2
Amp-3^{12}	1	2	6	3	6	10	28	80.0
Pgi-2^{12}	1	1	5	4	5	16	32	83.0
Pgi-2^{11}		1	6	4	6	9	26	81.6
Est-9^{12}		1	9	5	4	13	32	80.6
Est-9^{11}	1	1	3	3	8	13	29	84.1
Pgi-1^{12}	1	1	4	4	6	11	27	82.2
Pgi-1^{22}		1	8	4	6	15	34	82.3
Amp-2^{12}		1	6	6	7	13	33	82.7
Amp-2^{11}	1		6	2	4	8	21	79.6
Acp-1^{-4+9}	1		3	4	5	11	24	83.4
Acp-1^{+9+9}		2	9	4	7	15	37	81.5

[a] Pollen fertility was based on staining with acetocarmine
Note: The mean fertility was not significantly different between the two genotypes at each locus

those with partial pollen abortion (Table 4). The distribution of pollen fertility determined by pollen stainability was not correlated with segregation distortion for any of the isozyme or morphological markers. Pollen sterility based on pollen stainability may have no relation to the segregation distortion of marker genes in these experiments.

Measurement of pollen fertility and viability

Based on the ambiguous result obtained with respect to pollen fertility and segregation distortion at the marker loci examined, we investigated the relationship between pollen stainability and viability. Pollen of Indica-Japonica hybrids showed 45–55% stainable pollen. Yet, only 10% of the pollen of these hybrids germinated (Table 5, Fig. 1 C, D) as compared to 95% pollen germination in the parents. The extremely reduced germinability of pollen in the hybrids indicated that a large proportion of the pollen was inviable in spite of its normal appearance upon staining.

Table 5. Relationship between morphological evaluation of pollen and germinability of pollen in an artificial medium

Crosses	Germinability[a] (%)	Pollen stainability (%)
Akihikari	95.0±11.0	86.9
Tatumomoti	99.3± 1.3	98.9
IR36	94.2± 4.1	100
Akihikari/IR58	0.3± 0.5	47.3
Tatumimoti/IR50	8.1±10.0	48.0

[a] Confidence intervals were at 95% levels

Discussion

It is clear that many genes on several chromosomes cause segregation distortion in Indica-Japonica hybrids. Of the marker genes on the 7 chromosomes that we examined, those on chromosomes 3, 7, 8, 11 and 12 showed clear segregation distortion. With the exception of *Est-9*, alleles from the Indica parents showed dominance suggesting that characters from the Indica parent would be inherited at a higher frequency than those from the Japonica parent in Indica-Japonica crosses.

Segregation distortion due to partial abortion of the female gametes has been reported for marker genes on chromosome 6 linked with the *S-5* locus (Ikehashi and Araki 1986). A study of pollen development and the process of fertilization should offer insight into how selection via the male gametes results in segregation distortion at other loci. The distortion observed for markers on chromosome 4 (*lg* and *Ph*) and 11 (*Pgd-1*) should be able to be confirmed by further crossing and linkage analysis.

Although 45–55% of the pollen appeared to be morphologically abnormal in the Indica-Japonica hybrids studied, no linkage was detected between this trait and any of the markers showing distorted segregation in populations derived from these hybrids. Earlier studies by Nakagahra (1972, 1986) localized gametophyte gene loci on chromosome 3 on the basis of a clear distortion in the segregation of marker genes. They suggested that the gametophyte loci were responsible for the partial or total elimination of gametes carrying one of the alleles at that locus.

According to this hypothesis, gametes possessing the critical allele are sterile. As several gametophyte genes have been detected in our study of Indica-Japonica hybrids, any male gamete carrying such genes would be inviable despite its normal appearance upon staining. The significantly lowered germinability of pollen of such hybrids may be an indication of an abnormality attributable to the gametophyte genes.

The tighter the linkage between a marker locus and a gametophyte gene, the more extreme the segregation distortion is expected to be for that marker. Potentially, one allele of a marker gene would be totally absent from the population if the marker gene was tightly linked to a gametophyte gene and the gametophyte gene caused absolute inviability of the gamete.

Theoretically, if there are at least a few normal pollen grains in a floret, fertilization should occur, resulting in seed set. But the large number of abortive pollen grains in Indica-Japonica hybrids leads to failure in fertilization and reduced seed set.

The identification of neutral alleles at some gametophyte gene loci has practical implications. Such neutral alleles can be readily incorporated into Indica or Japonica parents with the aid of linked markers. Plant breeders attempting to recombine attributes from Indica and Japonica varieties would find it helpful to use these neutral alleles to overcome the problem of sterility in these crosses. It is clear from the data presented here that specific allelic combinations at any of a number of loci can cause sterility in Indica-Japonica hybrids. The identification of these alleles at these loci in specific varieties would be helpful in predicting whether or not sterility would be a problem in a particular hybrid combination. If tight linkages can be detected between these alleles and molecular markers, the identification of specific alleles in the donor varieties would become easier.

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